

# Reproductive anatomies of *Holospira* spp. (Gastropoda: Pulmonata: Urocoptidae) from Arizona and Sonora with a new subgenus and a new subspecies\*

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**Abstract.** The reproductive systems of seven species of *Holospira* from Arizona and Sonora, Mexico are illustrated and compared. They exhibit four different morphologies based on the size, shape and arrangement of the penial complex and the spermathecal duct. These four morphological groups represent lineages that do not completely correspond to the three presently recognized subgenera from this region.

*Sonoraloa* Gilbertson subg. nov. and *Holospira dentaxis alamellata* Gilbertson, ssp. nov. are described. *H. remondi* (Gabb, 1865), *H. dentaxis* Pilsbry, 1953 and *H. mazatlanica* (Bartsch, 1943) are transferred from subgenus *Allocoryphe* to *Sonoraloa*.

Land snails comprising the urocoptid genus *Holospira* von Martens, 1860, exhibit moderate-sized (ca. 8-20 mm in length), elongated, turritiform shells that retain their spire. They inhabit three southwestern states (Arizona, New Mexico, and Texas) and range southward through most of Mexico. Most species are very xerophytic and calcicolous. Three of the six subgenera recognized presently [*Allocoryphe* Pilsbry, 1946; *Eudistemma* (Dall, 1896); and *Holospira s.s.* von Martens, 1860] are represented in Arizona and Sonora, Mexico, the northwestern corner of the *Holospira* range.

The taxonomy of the genus is based entirely on shell characteristics such as overall size, whorl size, shape of the aperture, sculpture and aspects of the internal column. However, these characters tend to be somewhat unreliable for systematic studies due to their variability. Thompson (1964) suggested that true interspecific relationships within the genus are best determined by the soft anatomy. Unfortunately, holospiras are poorly known in this regard. Descriptions of the reproductive systems of only a few species (11) have been published (Pilsbry, 1903; Gilbertson, 1989a, b; Thompson, 1964). Five of these are from Arizona and Sonora, Mexico (Gilbertson, 1989a, b).

The present paper describes the reproductive anatomies of three additional *Holospira* species from Arizona and two from Sonora. The anatomical configuration of the soft parts of the two Sonoran species, along with aspects of the embryonic whorls of their shells, indicates a separate lineage which requires the description of *Sonoraloa* subg. nov.

## MATERIALS AND METHODS

Estivating snails were collected from under surface

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rocks and/or dead plant material (especially agaves and yuccas) usually in areas of limestone deposits. The Mexican species were collected at sites in central Sonora, between Hermosillo and Sahuaripa (Fig. 1), including the Sierra Batamote. In Arizona, collections were made in the Dragoon and Huachuca Mountains.

Mature specimens were immersed individually in a small vial of water for three to five days until drowned. The shell of each specimen was broken and removed carefully. Then the reproductive system of the animal was dissected free from the other internal organs and fixed in 70% ethanol. The reproductive organs were stained with Delafield Haematoxylin, destained with 3% acid alcohol, counter-stained with Eosin Y, and slide-mounted (see Gregg, 1959; Naranjo-Garcia, 1989). The reproductive systems of two to four specimens of each species were dissected and mounted.

Institutions cited in this article are abbreviated as follows: ANSP, Academy of Natural Sciences of Philadelphia; LACM, Los Angeles County Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History; UNAM, Universidad Nacional Autonoma de Mexico; USNM, United States National Museum-Smithsonian Institution.

## TAXONOMIC DESCRIPTIONS

Genus *Holospira* von Martens, 1860

Subgenus *Allocoryphe* Pilsbry, 1946

(Figures 2, 3a)

**Type species:** *Holospira (Allocoryphe) minima* von Martens, 1897, by original designation. The subgenus is monotypic.

**Type locality:** Cerro de la Campana, Hermosillo, Sonora, Mexico.

**Diagnosis:** Shell exhibits a rounded aperture, expanded

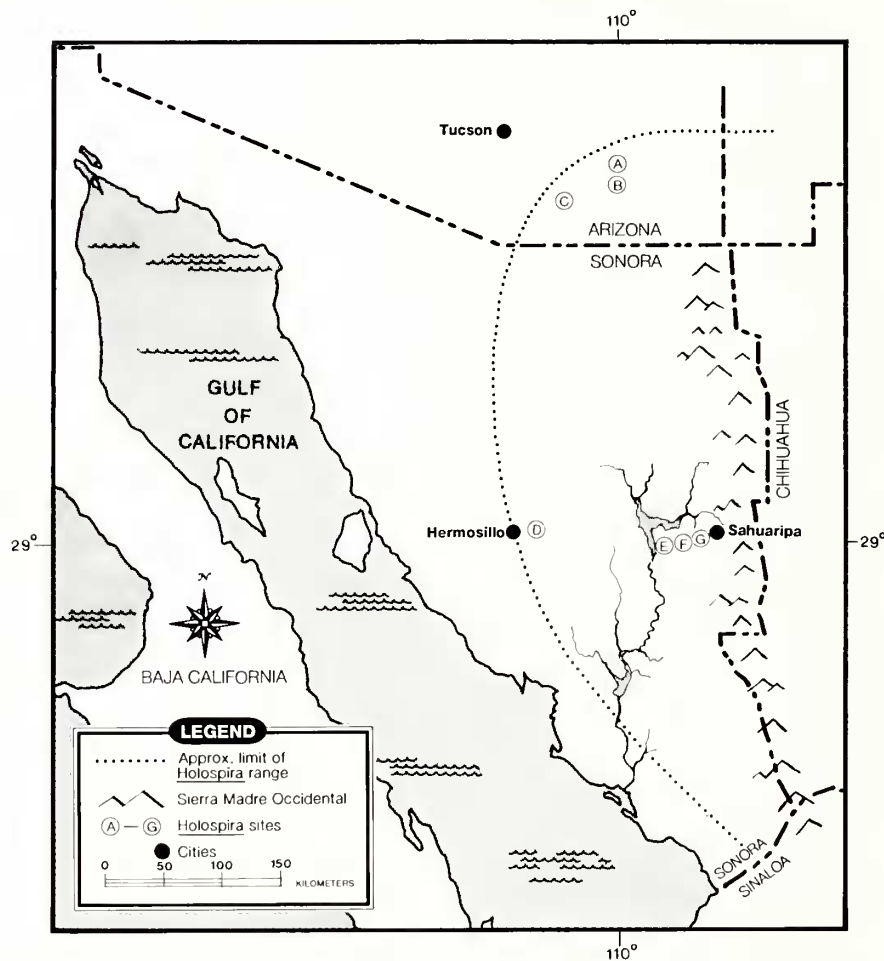


Fig. 1. Map of Arizona and Sonora, Mexico showing approximate locations of collecting sites of *Holospira* spp. discussed in this paper. A. *H. (Eudistemma) tantalus campestris*; B. *H. (E.) danielsi*; C. *H. (E.) ferrissi*; D. *H. (Allocoryphe) minima*; E. *H. (H.) milleri*; F. *H. (Sonoraloa) remondi laevior*; G. *G. (S.) dentaxis alamelata* spp. nov.

peristome, hollow ribs and a somewhat enlarged, alamelate, internal column. Embryonic whorls flat-sided and angular at the upper, outer margin. Male anatomy with tubular epiphallus inserting laterally into penis producing a penial caecum. Penial retractor muscle broad, inserting on apex of penial caecum.

**Material examined:** ANSP 166366, Cerro de la Campana, Hermosillo, Sonora, 55+ shells. SBMNH 35519, Cerro de la Mona, ca. 21 km east of Hermosillo, Sonora, N side of Hwy 15, 29°02.9'N, 110°39.4'W, elevation ca. 350 m, shell and slide-mounted reproductive system (illustrated specimens). SBMNH 35626, Cerro de la Mona (as above), 8 shells. LACM 88-354.1, Cerro de la Mona (as above), 7 shells.

**Remarks:** Pilsbry (1946) erected the subgenus *Allocoryphe* (allo, different; coryph, top) in a footnote for the "special group" of holospiras inhabiting northwestern Mexico, between the Sierra Madre Occidental and the Gulf of California (Fig. 1). This subgenus is restricted herein to *Holospira*

*minima*, which is the only *Holospira* species known to exhibit angular, embryonic whorls (i.e. a "different top"). These whorls are sculptured with "regularly spaced ribs that are overlaid by an open mesh of granular reticulations" (Thompson, 1988:92).

Subgenus *Sonoraloa* Gilbertson subg. nov.  
(Figs. 3c, 4, 5, 6, 7)

**Type species:** *Holospira remondi* (Gabb, 1865), designated herein. *H. remondi*, *H. dentaxis* Pilsbry, 1953, and *H. mazatlanica* (Bartsch, 1943) are transferred from subgenus *Allocoryphe*.

**Type locality:** 1.5 leagues (ca. 6 km) from Arivechi, Sonora, Mexico.

**Distribution:** Sonora and Sinaloa, Mexico.

**Diagnosis:** Shell generally similar to that of subgenus *Allocoryphe* with regard to aperture, peristome, and whorl size but differing by having one lamella (the axial), or none,

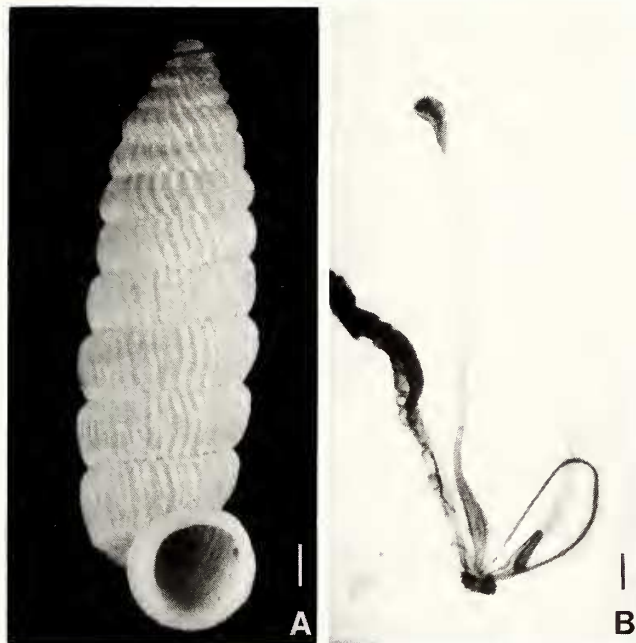


Fig. 2. *Holospira (Allocoryphe) minima*. A. Apertural view of shell. B. Reproductive system (except albumen gland and ovotestis) (scale bars = 1 mm).

on the internal column and having rounded, embryonic whorls. Male anatomy with a tubular epiphallus inserting apically on an ovate penis, adjacent to insertion of penial retractor muscle.

**Material examined:** ANSP 25046, *Holospira remondi*, 1.5 leagues (ca. 6 km) from Arivechi, Sahuaripe Valley, Sonora, one lectotype. ANSP 166484, *H. dentaxis*, drift at ford of Rio Yaqui about 17.5 km N of Ciudad Obregon, Sonora, holotype, 3 paratypes. USNM 381625, *H. mazatlanica*, drift at Mazatlan, Sinaloa, Mexico, 4 paratypes.

**Etymology:** *Sonoraloa* is a contraction of the names of the two northwestern Mexican states which comprise the known range of this subgenus, Sonora and Sinaloa.

**Remarks:** *Holospira dentaxis*, *H. mazatlanica* and possibly *H. remondi* (including numerous subspecies) were described on the basis of river drift shells. Because of this, it is very difficult to locate living populations. However, populations referable subspecifically to *H. remondi* and *H. dentaxis* have been located and their reproductive anatomies are discussed herein.

*Holospira kinonis* Baily and Baily, 1940, is the only other species that Pilsbry (1953) placed in the subgenus *Allocoryphe*. However, its shell is very slender and turritiform, giving it the external appearance of an *Epirobia*, and its embryonic whorls are rounded, but differ from those of the other species by not enlarging in diameter. Because of these shell features, and lack of anatomical data, its taxonomic status is uncertain.

*Holospira (Sonoraloa) remondi laevior* Pilsbry, 1953  
(Figs. 3c, 7)

**Synonym:** *Holospira remondi* (Gabb, 1865)

**Material examined:** ANSP 188316, *Holospira remondi laevior*, drift of Laguna Preza Rodriguez, Hermosillo, Sonora, holotype, 3 paratypes. SBMNH 35520, *H. remondi laevior*. Sierra Batamote, east-central Sonora (near El Milagro Mine), ca. 1,070 m, 20.2 km E of Rio Yaqui Bridge along Hwy 15 from La Estrella to Bacanora, 28°57.7'N, 109°30.5'W, Sonora, shell and slide-mounted reproductive system (illustrated specimens). SBMNH 35603, *H. remondi laevior*, Sierra Batamote (as above), 5 shells. LACM 88-355.1, *H. remondi laevior*, Sierra Batamote (as above), 6 shells.

**Remarks:** The cylindroconic shells of the present population from the Sierra Batamote are slightly longer (mean length = 14.6 mm for 11 shells) than that of holotype *H. remondi laevior* (length = 13.8 mm) but overlap occurs (range = 13.4 - 17.0 mm). Their somewhat inflated internal columns (ca. 0.18-0.20 of shell width) suggest a close relationship with genus *Coelostemma* Dall, 1895.

Bequaert (1973) synonymized *Holospira remondi laevior* (and all other subspecies) with the nominate subspecies without comment. It is considered valid herein due to the characteristically elongated, cylindrical portion of its shell.

*Holospira (Sonoraloa) dentaxis alamellata*  
Gilbertson ssp. nov.  
(Figs. 4-6)

**Diagnosis:** Shell comparable to *Holospira dentaxis dentaxis* Pilsbry, 1953, in overall shape, shape of the aperture, whorl size and sculpture but slightly larger and alamellate (holotype *H. d. dentaxis* is 11.0 mm in length, 3.5 mm in diameter, 13 whorls and has an axial lamella).

**Shell of holotype:** Shell medium-sized for genus, moderately cylindroconic in shape, convex with ninth whorl of greatest diameter, tan in color. Whorls very convex, 12.1 in number. Embryonic whorls 2.4 in number, rounded, minutely granular, increasing in diameter. All post-embryonic whorls sculptured with moderate-sized, solid, axial ribs which are slightly retractively slanted and arched, having intercostal spaces ca. three times width of ribs. Penultimate whorl with 31 ribs. Aperture slightly auriculate; peristome extended somewhat from body whorl and moderately expanded except on upper-outer margin. Umbilicus narrowly perforate. Internal column smooth, slightly expanded, increasing in diameter apically. Maximum length 11.7 mm, diameter 4.0 mm.

**Paratypes:** Seven paratypes vary from turritiform to cylindroconic in shape. They range from 10.9 to 11.9 mm in length (mean 11.5 mm) and 3.7 to 4.0 mm in diameter (mean 3.9). Radula: Radula typical for genus. Formula 16-6-1-6-16 (= 45

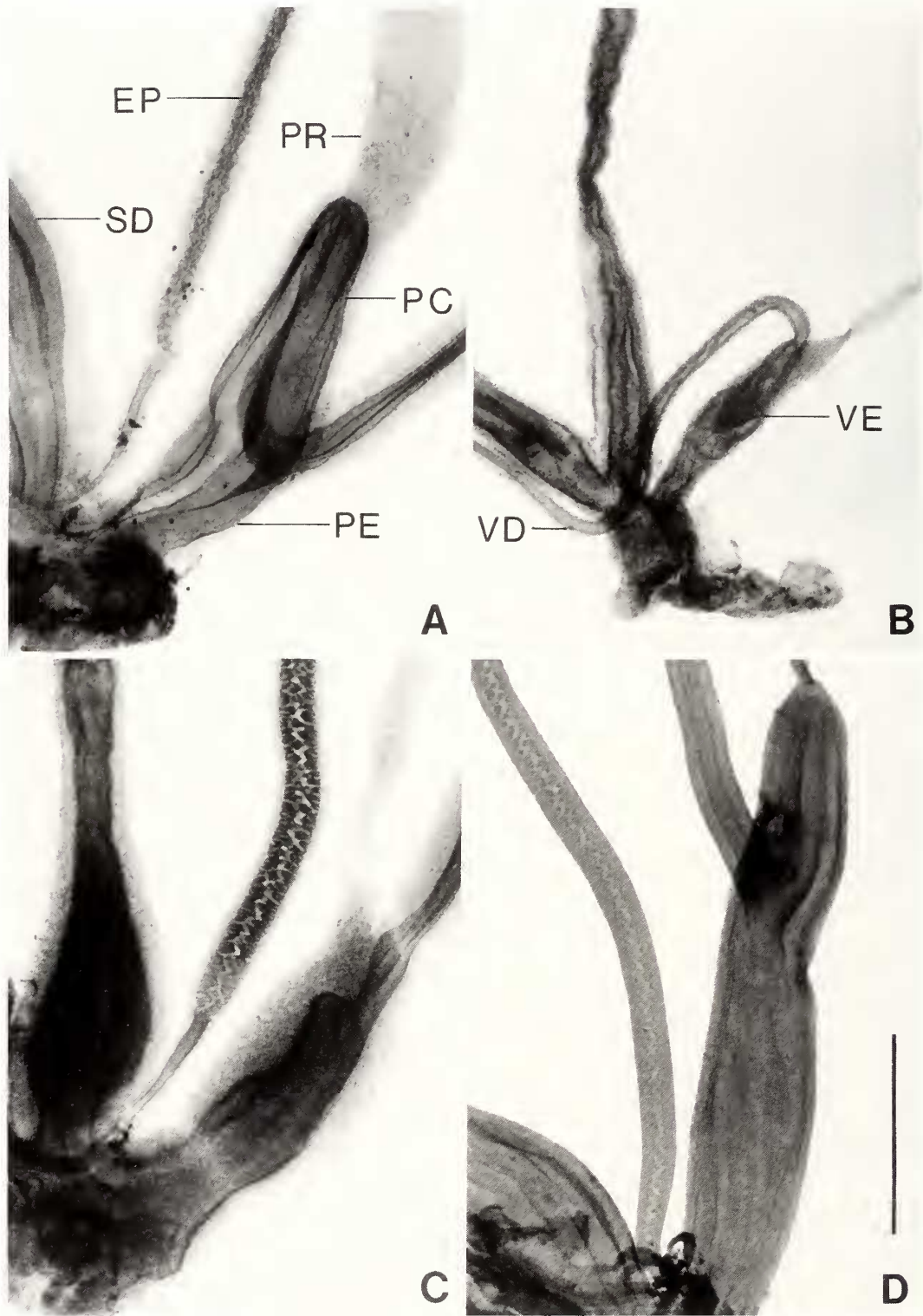


Fig. 3. Basal reproductive organs of *Holospira* spp. representing the four lineages discussed herein. A. *H. (Allocoryphe) minima*. B. *H. (Holospira) milleri*. C. *Holospira (Sonoraloa) remondi laevior*. D. *H. (Eudistemma) danielsi*. Abbreviations: EP, epiphallus; PC, penial caecum; PE, penis; PR, penial retractor muscle; SD, spermathecal duct; VD, vas deferens; VE, verge (scale bar = 1 mm).

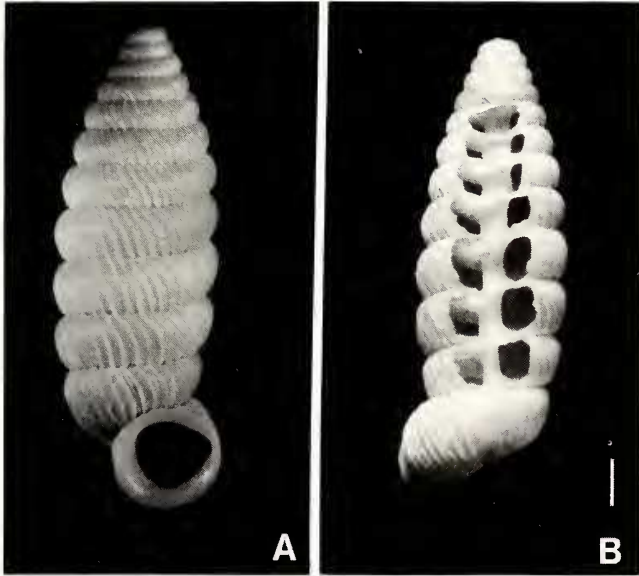


Fig. 4. *Holospira (Sonoraloa) dentaxis alamellata* ssp. nov. A. Apertural view of holotype. B. Dorsal view of paratype opened to show internal column (scale bar = 1 mm).

teeth per row).

**Reproductive system:** Penis small and slightly ovate due to a constriction at junction with genital atrium. Vas deferens enlarging into tubular epiphallus which inserts apically into penis. Spermathecal duct rounded basally with internal folds, proceeding apically into short constricted section, and then enlarging with scalloped-appearing interior; spermatheca tapering into duct. Spermathecal diverticulum lacking.

**Type locality:** Riperian gorge, S side of Hwy 15, 7.5 road km W of Sahuaripa, 29°01.5'N, 109°18.7'W, elevation ca. 700 m, Sonora Mexico.

**Disposition of types:** Holotype: SBMNH 35514. Paratypes: ANSP 389889; LACM 2246; UNAM-IB 190; USNM 860570. SBMNH 35515, slide-mounted reproductive system (illustrated specimen). SBMNH 35593, 35594, two slide-mounted reproductive systems.

**Etymology:** This subspecies is named for the absence of lamellae on the internal column.

**Remarks:** *Holospira dentaxis dentaxis* Pilsbry, 1953, *H. d. lamellaxis* Pilsbry, 1953, *H. d. striatella* Pilsbry, 1953 and *H. d. pomatia* Pilsbry, 1953 were described on the basis of drift shells from the mouth of the Rio Yaqui. Bequaert (1973) synonymized all subspecies with the nominate subspecies.

#### DESCRIPTIONS OF REPRODUCTIVE ANATOMIES

*Holospira* species inhabiting Arizona and Sonora, Mexico exhibit at least four distinctly different arrangements (= lineages) of the reproductive system based on variations

of the male genitalia and the female spermathecal duct. Other female organs such as the free oviduct, uterus and albumen gland are morphologically similar, varying only in length. In all cases, the spermathecal duct is completely separate from the free oviduct; hence, a vagina is lacking. A spermathecal diverticulum is present in the Arizona species (lineage 1) and is lacking in all three of the Sonoran groups (lineages 2-4).

LINEAGE 1: Subgenus *Eudistemma* (Dall, 1896)

*Holospira (Eudistemma) danielsi* Pilsbry and Ferriss, 1915 (Figs. 8, 9)

**Material examined:** SBMNH 35516, foothills on N side of mouth of Cochise Stronghold Canyon West, Dragoon Mts., 31°56.0'N, 110°00.1'W, elev. ca. 1615 m, Cochise Co., Arizona (at or near type locality), one slide-mounted reproductive system (illustrated specimen). SBMNH 35595, 35596 (data as above), two slides.

**Reproductive system:** The male anatomy is characterized by

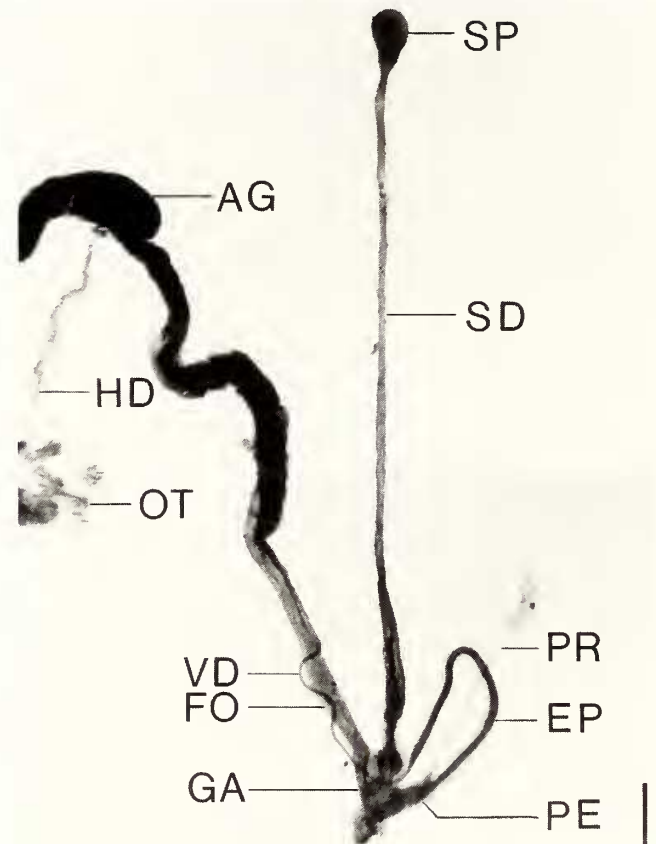


Fig. 5. Reproductive system of *Holospira (Sonoraloa) dentaxis alamellata* ssp. nov. Abbreviations: AG, albumen gland; EP, epiphallus; FO, free oviduct; GA, genital atrium; HD, hermaphroditic duct; OT, ovotestis; PE, penis; PR, penial retractor muscle; SD, spermathecal duct; SP, spermatheca; VD, vas deferens (scale bar = 1 mm).



Fig. 6. Basal reproductive organs of *Holospira (Sonoraloa) dentaxis alamellata* sp. nov. Abbreviations: EP, epiphallus; PE, penis; SD, spermathecal duct (scale bar = 1 mm).

an elongate penis which contains slight internal folds of tissue. The apical portion of the penis is a caecum due to the lateral insertion of the epiphallus. The epiphallus is an elongate (Appendix 1), tubular enlargement of the vas deferens which contains a serrate-appearing, glandular endothelium in its proximal portion. The penial retractor muscle is rather slender, and inserts on the rounded (dome-shaped) apex of the penial caecum. The spermathecal duct is characterized by a diverticulum and an elongate, gradually tapering spermatheca. A retractor muscle inserts on the basal portions of the oviduct and spermathecal duct.

*Holospira (Eudistemma) tantalus campestris* Pilsbry and Ferriss, 1915 (Figs. 8, 10)

**Synonym:** *Holospira campestris* Pilsbry and Ferriss, 1915  
**Material examined:** SBMNH 35517, Wood Canyon near a rock quarry, NW end of Dragoon Mountains, 32°00.5'N,

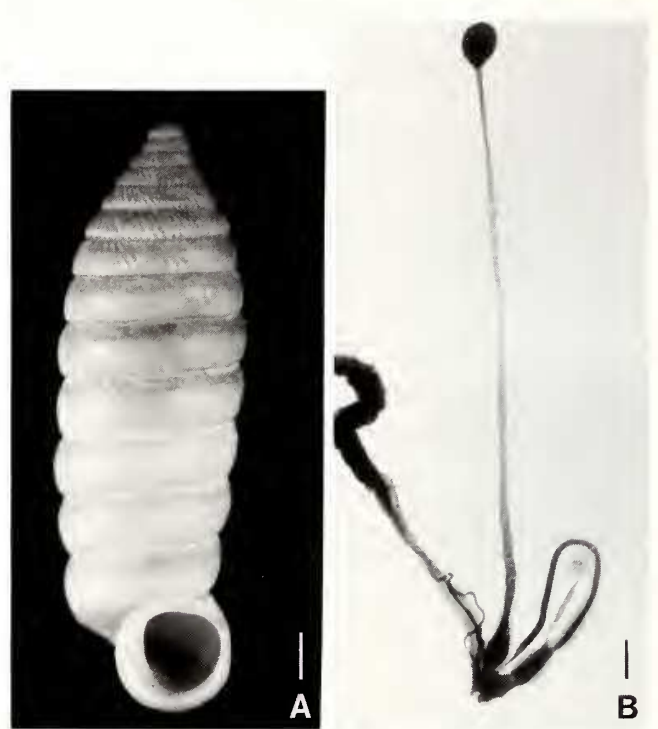


Fig. 7. *Holospira (Sonoraloa) remondi laevior*. A. Apertural view of shell. B. Reproductive system (excluding albumen gland and ovotestis) (scale bars = 1 mm).

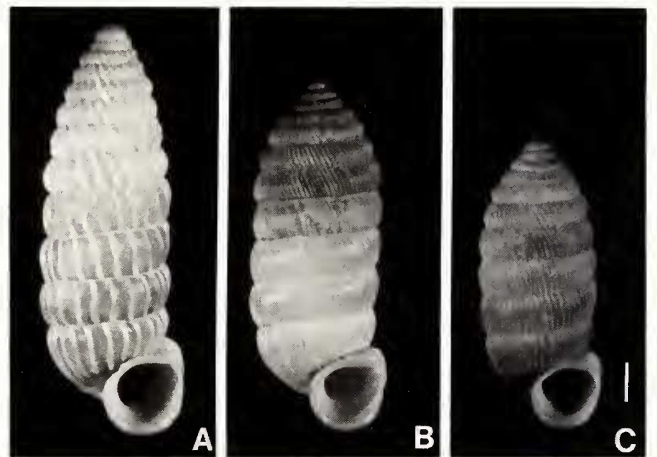


Fig. 8. Apertural view of three Arizona *Holospira* species. A. *Holospira (Eudistemma) danielsi*. B. *H. (E.) tantalus campestris*. C. *H. (E.) ferrissi* (scale bar = 1 mm).

110°00.2'W, elevation ca. 1640 m, Cochise Co., Arizona, one slide-mounted reproductive system (illustrated specimen). SBMNH 35597 (data as above), one slide.

**Reproductive system:** Similar to *H. danielsi* except: 1) the spermathecal duct is longer and more slender (including the base); 2) the epiphallus is longer and more slender; 3) the

apex of the penial caecum is tapered; 4) the penis lacks internal folds.

*Holospira (Eudistemma) ferrissi* Pilsbry, 1905 (Figs. 8, 11)  
**Material examined:** SBMNH 35518, foothills immediately SE of Manila Mine, NW end of Huachuca Mts., 31°33.2'N, 110°26.2'W, elev. ca. 1620 m, Cochise Co., Arizona (type locality), one slide-mounted reproductive system (illustrated specimen). SBMNH 35598 (data as above), one slide.

**Reproductive system:** Similar to *Holospira (Eudistemma) danielsi* except that: 1) the system is smaller overall (ca. 0.70); 2) the basal portion of the spermathecal duct is distinctly rounded; 3) the apex of the penial caecum is tapered and; 4) the penis lacks internal folds.

**Remarks:** *Eudistemma* (see Bequaert and Miller, 1973:138) is the primary subgenus of *Holospira* in Arizona. It inhabits a small southeastern corner of the state and extends eastward through southern New Mexico into northwestern Texas. One population referable to *H. (E.) ferrissi* Pilsbry, 1905 has been located in extreme northern Sonora (Bequaert and Miller, 1973).

*Holospira (Eudistemma) danielsi*, *H. (E.) ferrissi* and *H. (E.) tantalus campestris*, exhibit similar reproductive systems. The comparable systems of two other species in subgenus *Eudistemma*, namely *H. (E.) arizonensis* and *H. (E.) chiricahuana* Pilsbry, 1905, have been published (Gilbertson, 1989b). *H. arizonensis* has a slender (including the base), elongated (14.8 mm in the described specimen) spermathecal duct which closely resembles that of *H. tantalus campestris*. *H. chiricahuana* exhibits distinct undulated internal folds in the penis and lower spermathecal duct that are not apparent in the presently described species (nor in *H. arizonensis*). A retractor muscle inserting on the basal female structures is present in all species observed. The majority of the muscle was eliminated during dissection of the photographed specimens of *H. tantalus campestris* and *H. ferrissi*.

*Holospira (Holospira) sherbrookei* Gilbertson, 1989, from the Chiricahua Mountains, exhibits a reproductive system that corresponds with those of *Eudistemma* spp. It is placed in *Holospira s.s.* because of its quadrilamellate shell condition.

The *Eudistemma* reproductive system is somewhat comparable to that of snails in subgenus *Bostricocentrum* Strebel, 1880, from southern Mexico (Thompson, 1964). Snails in both subgenera exhibit a spermathecal diverticulum, an elongate spermatheca and a long, slender, tubular epiphallus. However, in *Bostricocentrum* the epiphallus inserts apically into the penis and the penis exhibits a terminal knob for the attachment of the retractor muscle.

LINEAGE 2: Subgenus *Allocoryphe* Pilsbry, 1946  
*Holospira (Allocoryphe) minima* (Figs. 2, 3a)

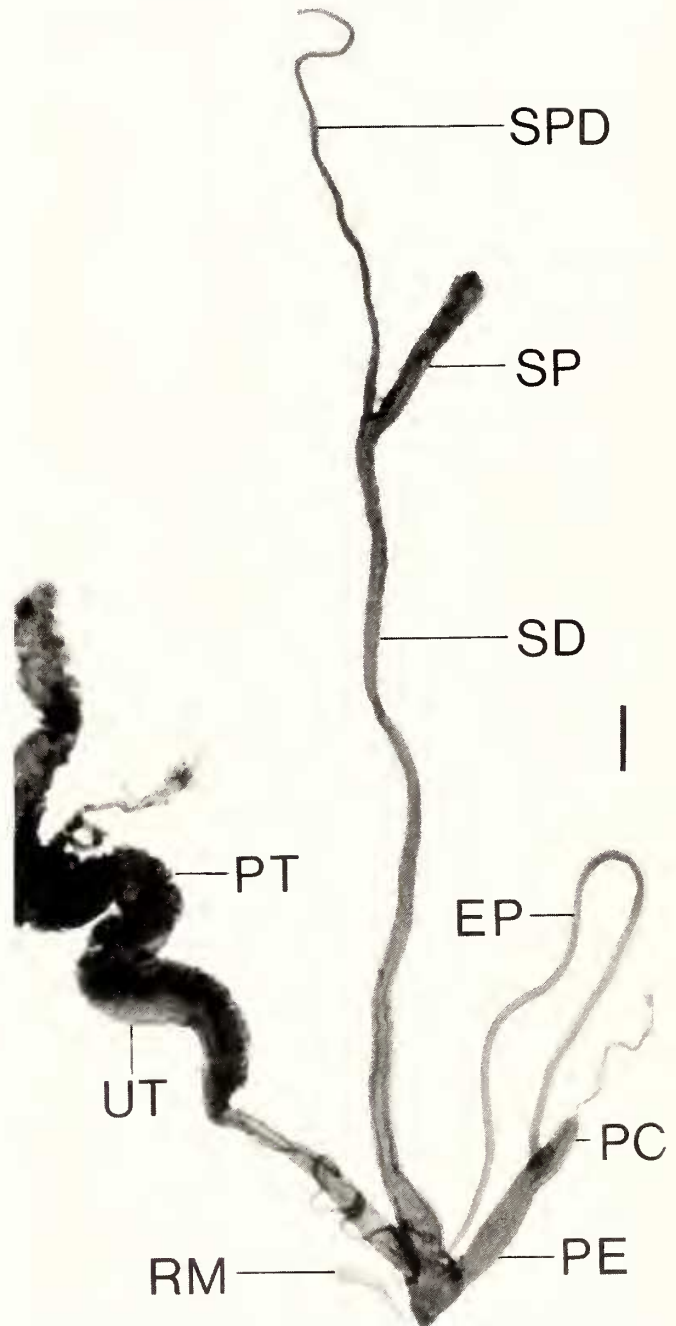


Fig. 9. Reproductive system of *Holospira (Eudistemma) danielsi* (except ovotestis). Abbreviations: EP, epiphallus; PC, penial caecum; PE, penis; PT, prostate gland; RM, retractor muscle; SD, spermathecal duct; SP, spermatheca; SPD, spermathecal diverticulum; UT, uterus (scale bar = 1 mm).

**Material examined:** SBMNH 35519, Cerro de la Mona, ca. 21 km east of Hermosillo, Sonora, N side of Hwy 15, 29°02.9'N, 110°39.4'W, elevation ca. 350 m, one slide-mounted reproductive system (illustrated specimen). SBMNH

35599, 35600 (data as above), two slides.

**Reproductive system:** The male anatomy is characterized by the presence of a stout, tubular epiphallus which inserts laterally into the penis producing an apical penial caecum. This caecum is ca. two-thirds of the total penis length and (along with the penis proper) contains internal folds of tissue.



Fig. 10. Reproductive system of *Holospira (Eudistemma) tantalus campestris* (except ovotestis) (scale bar = 1 mm).

The penial retractor muscle attaches to the apex of the penial caecum and is unusually broad. The spermathecal duct is inflated basally and its spermatheca tapers into the duct.

**Remarks:** *Holospira minima* is the only species known to exhibit this morphology of the reproductive system. It appears to correlate with the presence of its distinctive, embryonic whorls.

**LINEAGE 3:** Subgenus *Sonoraloa* Gilbertson, subg. nov. *Holospira (Sonoraloa) remondi laevior* Pilsbry, 1953 (Figs. 3c, 7)

**Material examined:** SBMNH 35520, Sierra Batamote, east-central Sonora (near El Milagro Mine), ca. 1,070 m, 20.2 km E of the Rio Yaqui Bridge along Hwy 15 from La Estrella to Bacanora, 28°57.5'N, 109°30.5'W, Sonora, Mexico, one slide-mounted reproductive system (illustrated specimen). SBMNH 35601, 35602 (data as above), two slides.

**Reproductive system:** The male anatomy is characterized by a vas deferens that enlarges abruptly into a tubular epiphallus. It continues to enlarge distally before inserting apically into the penis. The penis is ovate, constricting at its junction with the genital atrium and exhibits a diagnostic internal outline. The penial retractor muscle is moderate in size, inserting apically onto the penis, adjacent to the epiphallus. The spermathecal duct is expanded basally (ca. same size as penis), and proceeds apically into an internally convoluted section; the spermatheca is oval-shaped.

**Remarks:** The penial complex of *Holospira (Sonoraloa) remondi laevior* is similar to that of *H. (S.) dentaxis alamellata* ssp. nov. They differ from the male anatomy of *H. (Allocoryphe) minima* by: 1) the apical insertion of the epiphallus into the penis, 2) the oval shape of the penis and 3) the narrower (ca. one-half to one-third width) penial retrac-

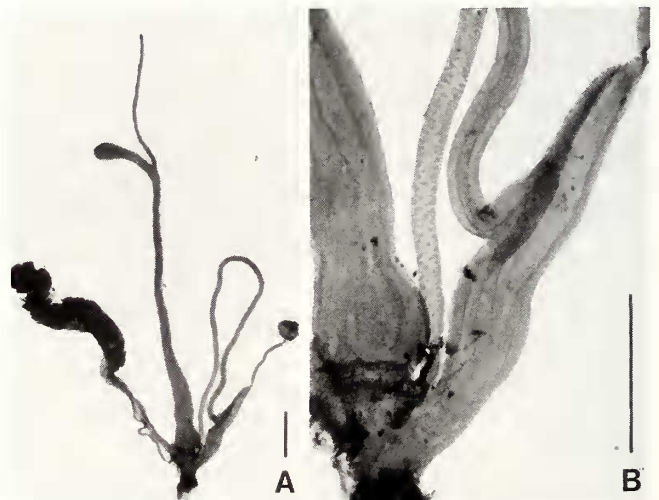


Fig. 11. Reproductive system of *Holospira (Eudistemma) ferrissi* (except ovotestis). A. Entire system. B. Basal anatomy (scale bars = 1 mm).



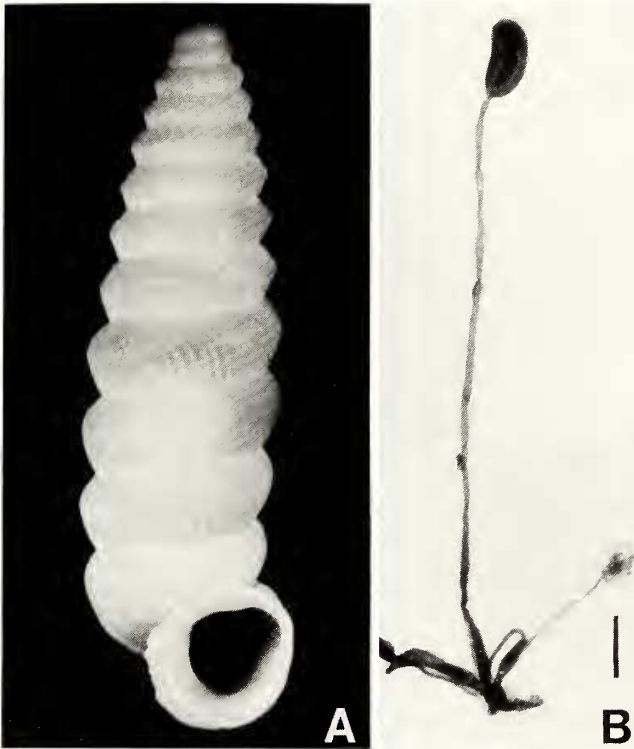


Fig. 12. *Holospira* (*H.*) *milleri*. A. Apertural view of shell. B. Male reproductive system and female spermathecal duct (scale bar = 1 mm).

tor muscle. These differences confirm the validity of *Sonoraloa* subg. nov.

LINEAGE 4: *Holospira* s.s. von Martens, 1860  
*Holospira* (*Holospira*) *milleri* Gilbertson, 1989  
 Figs. 3b, 12)

**Material examined:** SBMNH 35521, E side of Rio Yaqui in a ravine near mouth of El Alamo Wash, ca. 1.5 km S of the military footbridge at El Novillo; 28°58.1'N, 109°37.5'W, elev. ca. 260 m, Sonora, Mexico (type locality), one slide-mounted reproductive system (illustrated specimen). SBMNH 35604, 35605, 35606 (data as above), three slides (two specimens possibly immature).

**Reproductive system:** See Gilbertson (1989a) for original description. The male system exhibits a small penial sac which contains a verge. The vas deferens inserts into a short, conic epiphallus atop the penial sac. The basal portion of the spermathecal duct typically contains an undulated, internal lumen although it is not seen on the illustrated specimen. The spermatheca is indented medially (reniform) and constricted basally before joining the spermathecal duct.

**Remarks:** The male anatomy of *Holospira* (*H.*) *milleri* is dramatically different from that of all other described *Holospira* spp. (for which the anatomy is known). It is the

only species that exhibits a verge in the penial sac and whose vas deferens does not enlarge into a tubular epiphallus.

An undescribed "form" with a trilamellate shell was discovered at the same site as *Holospira* (*Sonoraloa*) *remondi laevior* in the Sierra Batamote. Its anatomy is very similar to that of *H. (H.) milleri* (including the presence of a verge). However, because of the trilamellate shell condition, this "form" cannot be included in *Holospira* s.s. (along with *H. milleri*) as the subgenus is defined at present (quadrilamellate only).

The reproductive systems of three additional species assigned to subgenus *Holospira* s.s. have been published (Pilsbry, 1903; Gilbertson, 1989b). They are *H. (H.) sherbrookei* Gilbertson, 1989 from Arizona, *H. (H.) goldfussi* (Menke, 1847) from Texas and *H. (H.) nelsoni* Pilsbry, 1903 from Coahilla, Mexico. They exhibit arrangements of the reproductive system that are significantly different from *H. (H.) milleri* and from each other. Hence, it is apparent that *Holospira* s.s. is polyphyletic and in need of revision.

## CONCLUDING REMARKS

Studies of the reproductive system indicate a greater than anticipated number of *Holospira* lineages from the northwestern corner of its range. Additional field work, especially in Mexico, is necessary for continued systematic evaluation of the genus. Examination of the soft anatomies of living populations is essential for an adequate understanding of their phylogeny. Eventually, the taxonomy of the entire genus should be revised to include anatomical data.

## ACKNOWLEDGMENTS

I sincerely thank Edna Naranjo-Garcia, James E. Hoffman and Walter B. Miller for accompanying me on collecting expeditions including one to Sonora at which time we returned to sites of *Holospira* populations discovered many years earlier by Dr. Miller. These populations represent the Sonoran species whose anatomies are described herein. I also thank M. Andria Garback at the Philadelphia Academy of Sciences and Paul R. Greenhall at the National Museum of Natural History; Smithsonian Institution for the loan of type material of Sonoran *Holospira* spp. and Dwayne L. Moses for assistance with the illustrations. Dr. Miller and three anonymous reviewers offered many helpful suggestions. In addition, I thank the Professional Development Institute of Orange Coast College for awarding me partial release time from teaching duties for the preparation of this manuscript.

## LITERATURE CITED

- Baily, J. L. and R. I. Baily. 1940. A new urocoptid mollusc from the State of Sonora, Mexico. *Nautilus* 53(3):94-95; Pl. 12, Fig. 1.  
 Bartsch, P. 1943. Notes on Mexican urocoptid mollusks. *Journal of the Washington (D.C.) Academy of Sciences* 33(2):54-59.  
 Bequaert, J. C. and W. B. Miller. 1973. *The Mollusks of the arid Southwest with an Arizona check list*. University of Arizona Press, Tucson, Arizona. i-xvi + 271 pp.

- Dall, W. H. 1895. Synopsis of the subdivisions of *Holospira* and some related genera. *Nautilus* 9(5):50-51.
- Dall, W. H. 1896. Diagnoses of new mollusks from the Survey of the Mexican Boundary. *Proceedings of the United States National Museum* 18(1033):1-6.
- Gabb, W. M. 1865. Descriptions of three new species of Mexican land shells. *American Journal of Conchology* 1(3):208-209, Pl. 19.
- Gilbertson, L. H. 1989a. A new species of *Holospira* (Gastropoda: Pulmonata) from Sonora, with the reproductive anatomy of *Holospira minima*. *Veliger* 32(1):91-94.
- Gilbertson, L. H. 1989b. A new species of *Holospira* (Gastropoda: Pulmonata) from Arizona, with the reproductive anatomies of *H. arizonensis* and *H. chiricahuana*. *Veliger* 32(3):308-312.
- Gregg, W. O. 1959. A technique for preparing in-toto mounts of molluscan anatomical dissections. *Annual Report of the American Malacological Union for 1958* 25:39.
- Naranjo-Garcia, E. 1989. Four additional species of *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from Sonora, Mexico. *Veliger* 32(1):84-90.
- Martens, E. von. 1860. *Die Heliceen nach Natürlicher Verwandtschaft systematisch geordnet von Joh. Christ. Albers*. 2nd edition. Berlin. 359 pp.
- Martens, E. von. 1890-1901. *Biologia Centrali Americana. Terrestrial and Fluvial Mollusca*. London. i-xxviii + 1-706 (1897:249-288), Pls. 1-44.
- Menke, K. T. 1847. Vier neue Arten der Gattung *Cylindrella* Pfr. *Zeitschrift für Malakozoologie* 4:1-3.
- Pilsbry, H. A. 1903. *Manual of Conchology* (2) 15, Urocoptidae. Philadelphia i-viii + 323 pp.
- Pilsbry, H. A. 1905. Mollusca of the southwestern States. I. Urocoptidae; Helicidae of Arizona and New Mexico. *Proceedings of the Academy of Natural Sciences of Philadelphia* 57:211-290, pls. 11-27.
- Pilsbry, H. A. 1946. Land Mollusca of North America. *Monographs of the Academy of Natural Sciences of Philadelphia* 3,2(1):i-iv + 520 pp.
- Pilsbry, H. A. 1953. Inland Mollusca of Northern Mexico. II. Urocoptidae, Pupillidae, Strobilopsidae, Valloniidae, and Cionellidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 105:133-167, pls. 3-10.
- Pilsbry, H. A. and J. H. Ferriss. 1915. Mollusca of the southwestern States. VII. The Dragoon, Mule, Santa Rita, Baboquivari and Tucson Ranges, Arizona. *Proceedings of the Academy of Natural Sciences of Philadelphia* 67:363-418, pls. 8-15.
- Strebel, H. and G. Pfeiffer. 1880. *Beitrag zur Kenntniss der Fauna Mexikanischer Land und Süsswasser-Conchylien*, pt. IV. Hamburg. 1-112 pp. 15 pls.
- Thompson, F. G. 1964. Systematic studies on Mexican land snails of the genus *Holospira*, subgenus *Bostricocentrum*. *Malacologia* 2(1):131-143.
- Thompson, F. G. 1988. The hollow-ribbed land snails of the genus *Coelostemma* of the southwestern United States and Mexico. *Bulletin of the Florida State Museum: Biological Sciences* 33(2):87-111.

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## APPENDIX 1.

Measurements (mm) of *Holospira* reproductive anatomies figured herein.

Species	Penis	Penial Retr. Muscle	Epi-phall.	Sperma-thecal Duct	Sperma-thecal Divert.	Sperma-theca	Free Ovid.
<i>H. danielsi</i>	3.0	2.5	11.0	12.6	6.0	2.4	3.8
<i>H. dentaxis alamellata</i>	0.6	3.3	5.5	13.4	-	1.2	4.8
<i>H. ferrissi</i>	2.7	1.7	11.0	8.2	4.0	1.8	2.3
<i>H. milleri</i>	0.6	1.9	0.3	10.9	-	1.5	4.1
<i>H. minima</i>	2.0	3.0	8.2	12.1	-	1.6	3.8
<i>H. remondi laevior</i>	1.5	2.0	7.4	16.8	-	1.3	3.7
<i>H. tantalus campestris</i>	3.9	5.0	19.0	15.3	7.3	3.6	6.3

## APPENDIX 2.

Measurements (mm) of *Holospira* shells figured herein.

Species	Height	Width
<i>H. danielsi</i>	11.7	3.9
<i>H. dentaxis alamellata</i>	11.7	4.0
<i>H. ferrissi</i>	8.1	3.4
<i>H. milleri</i>	13.1	3.7
<i>H. minima</i>	14.5	4.5
<i>H. remondi laevior</i>	14.5	4.7
<i>H. tantalus campestris</i>	10.0	3.8

## APPENDIX 3.

Revised taxonomy of the genus *Holospira* from Arizona, Sonora and Sinaloa (\*indicates those species for which the reproductive system has been described).Subgenus *Holospira**H. cyclostoma**H. milleri*\**H. sherbrookei*\*Subgenus *Allocoryphe**H. minima*\*Subgenus *Sonoraloa* subg. nov.*H. remondi*\**H. dentaxis*\**H. mazatlanica*Subgenus *Eudistenma**H. arizonensis*\**H. chiricahuana*\**H. danielsi*\**H. ferrissi*\**H. millistriata**H. tantalus*\**H. whetstonensis**Incertae sedis**H. kinonis*